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Neuronal Processing Delays Are Compensated in the Sensorimotor Branch of the Visual System

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Summary

Moving objects change their position until signals from the photoreceptors arrive in the visual cortex. Nonetheless, motor responses to moving objects are accurate and do not lag behind the real-world position [1]. The questions are how and where neural delays are compensated for. It was suggested that compensation is achieved within the visual system by extrapolating the position of moving objects [2]. A visual illusion supports this idea: when a briefly flashed object is presented in the same position as a moving object, it appears to lag behind [3, 4]. However, moving objects do not appear ahead of their final or reversal points [5–7]. We investigated a situation where participants localized the final position of a moving stimulus. Visual perception and short-term memory of the final target position were accurate, but reaching movements were directed toward future positions of the target beyond the vanishing point. Our results show that neuronal latencies are not compensated for at early stages of visual processing, but at a late stage when retinotopic information is transformed into egocentric space used for motor responses. The sensorimotor system extrapolates the position of moving targets to allow for precise localization of moving targets despite neuronal latencies.

Results and Discussion

In the first experiment, observers fixated on a central fixation mark while we presented a moving target in the lower visual field (Figure 1). The target moved at one of three velocities (11.3, 18.8, and 26.3 deg/s) and disappeared at an unpredictable position. The perceived final target position was gauged in two different ways. Observers reached toward the final target position (motor condition) or they compared the final target position with the position of a probe stimulus (perceptual condition) that appeared 0.5 s after target offset. Reaching movements required transformation of the retinotopic target position into egocentric coordinates, whereas the comparison between target and probe was possible in retinotopic coordinates. Because the entire experiment took place in darkness, observers could not see their hands. Therefore, retinotopic and egocentric localization were completely separated.

There was a significant spatial error in the direction of motion when subjects pointed to the target's endpoint (t-tests, ps < 0.0001). The spatial error in the perceptual condition was not significantly (ps > 0.09) different from zero (see Figure 2A). The spatial error for motor judgments was, on average, 1 ± 0.19 deg SEM larger than with perceptual judgments ($p < .0001$). The experiment was run in two different versions to control for possible effects of losing stable retinal references in the dark. In one group of participants, the fixation point was extinguished when the target vanished; in the other it remained visible until the response was collected. Since the presence of stable reference had no effect, the two groups were combined in the above analysis ($n = 15$).

The results suggest that the target's position is extrapolated when the retinotopic target position is transformed into egocentric target position used for reaching movements, whereas retinotopic position judgments are accurate. Sensorimotor extrapolation may assure that reaching movements are on target despite neuronal delays; however, they introduce a spatial error that is not present in perceptual judgments. This finding is counter to the widely held belief that spatial information used for motor judgments is more accurate than that used for perceptual/cognitive judgments, such as the "same-different" judgments employed here [8]. This idea has been modified by authors claiming that motor judgments become more error prone when responses are slow or delayed because the influence of the cognitive system increases [9, 10]. In the present paradigm, motor responses had to be inhibited until target offset such that the average time from target offset to response completion, referred to as movement time, was rather long (925 ± 22 ms). However, further analysis of our data argues against the hypothesis that sensorimotor extrapolation depends on the speed of the response. Each observer's responses were classified as fast (840 ± 22 ms) or slow (1008 ± 22 ms) by median split. The spatial error did not depend on the relative speed. Similarly, there were no differences between fast and slow participants.

The position of the moving target may have been extrapolated by a fixed spatial distance across target velocities or by a fixed temporal interval. The temporal error can be calculated by dividing the spatial error through the respective target velocity. It indicates how much time into the future the target's trajectory was extrapolated. If the position was extrapolated by a constant distance, effects of velocity on the spatial error should be absent and the extrapolated time should consequently decrease with increasing velocity. In contrast, if the position was extrapolated by a constant time interval, there should be an effect of velocity on the spatial error but no effect on the temporal error. The results do not provide a clear answer. The spatial error increased by 0.5 deg with increasing velocity ($F[2, 28] = 27.53$, $p < 0.0001$), and the extrapolated time decreased with increasing velocity ($F[2, 28] = 9.89$, $p < 0.001$) and was 74, 63, and 51 ms ($M = 63$ ms) for velocities of 11.3, 18.8, and 26.3 deg/s, respectively. Thus, neither model

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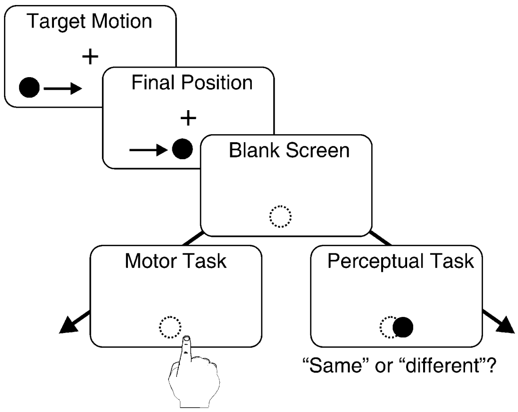

Figure 1. Schematic Drawing of the Experimental Procedure

In experiment 1, observers fixated on a central fixation mark while a target moved in the lower visual field and disappeared at an unpredictable position. In the motor task, observers reached toward the final target position. The deviation of the endpoint from the true final target position was recorded. In the perceptual task, a probe appeared and observers judged whether the probe was in the same or in a different position with respect to the final target position.

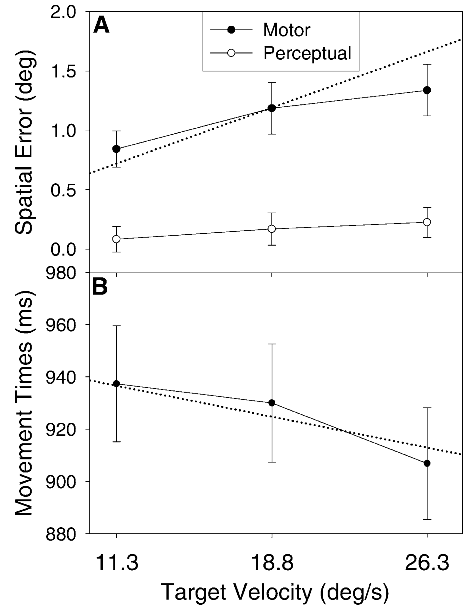

Figure 2. Results of the First Experiment

Error bars indicate the between-subjects standard error of the mean. A positive spatial error in (A) indicates that the judged target position was displaced in the direction of motion. Whereas perceptual judgments did not deviate significantly from zero, the endpoint of reaching movements showed substantial displacement in the direction of motion. There was an increase of the spatial error with velocity, but this increase fell short of the increase expected if the target position was extrapolated by a constant time interval (dotted line). (B) shows the mean time between target offset and contact with the screen. The dotted line indicates the decrease in movement time that would compensate for the deviations of the spatial error from constant extrapolation time.

is fully supported by the data. However, it is interesting to note that the reduced temporal extrapolation with increasing velocity may have been compensated for by faster responses to faster target speeds. As shown in Figure 2B, movement time decreased ($F[2, 26] = 10.83$, $p < .0005$) at a similar rate as the extrapolated time, which may favor the hypothesis of constant temporal extrapolation.

These results raise the question of whether retinal target motion is really necessary for sensorimotor extrapolation. To this end, we asked observers to fixate on a target that was surrounded by a large frame. In one condition, the target moved while the frame was stationary (real motion). In the other condition, the target was stationary, and the frame moved (induced motion). In complete darkness, the moving frame is incorrectly perceived as stationary, whereas the stationary target appears to move in a direction opposite to frame motion. Bridgeman et al. argued that induced motion deceives the perceptual/cognitive system, but not the motor system [11]. Even though this view has been criticized [1], there is an ongoing debate about whether the motor system is susceptible to illusory spatial information [10, 12, 13]. Here, we investigated whether motion signals arising from the combination of contextual cues in the absence of low-level motion in V1 is sufficient to elicit sensorimotor extrapolation.

The spatial error in the direction of motion was larger with motor than with perceptual judgments ($ps < 0.001$). Subjects do indeed extrapolate the illusory motion of a stationary target in reaching movements. Because the spatial error in the real-motion condition was also slightly different from zero with perceptual judgments (see below), the net sensorimotor extrapolation was calculated by subtracting perceptual from motor error. The net sensorimotor extrapolation with real motion was 0.78 ± 0.13 deg corresponding to a temporal error of 557 ms with respect to the peak velocity of 1.4 deg/s. The temporal error is implausibly large, which supports the hypothesis of constant distance extrapolation. The sensorimotor system may extrapolate a distance on the order of 1 deg of visual angle. Another possibility is that interactions between (illusory) eye movement signals and manual responses magnified extrapolation. Note that in contrast to peripheral target presentation, observers pursued the real motion of the target or had the illusory impression of doing so [14].

In this experiment, we imposed a time limit in the motor condition, resulting in movement times of 976 ± 34 deg and prolonged the time interval between target offset and probe onset in the perceptual condition to 1 s. Thus, the delays in the perceptual and motor conditions were approximately matched. In another group of participants, observers responded at leisure in the motor condition, which prolonged movement time to 1562 ± 114 ms, while the time interval in the perceptual condition was 0.5 s. Thus, the temporal delays in the perceptual and motor tasks were approximately matched in the former condition and differed grossly in the latter condition. However, the results did not differ between the matched (reported in the text and Figure 3A) and unmatched (shown in Figure 3B) conditions, indicating that memory does not play a role for our results.

With induced motion, the difference between perceptual and motor judgments may be attributed to sensori-

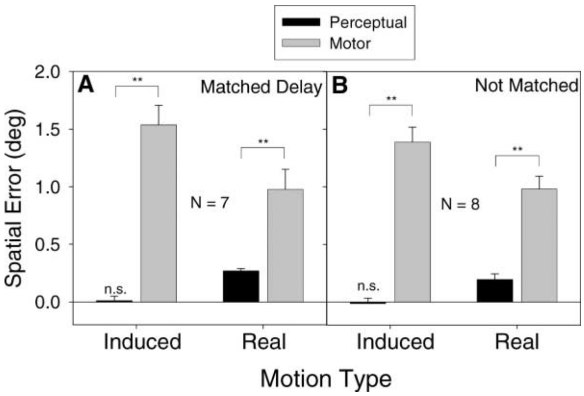

Figure 3. Results of the Second Experiment

In the second experiment, the spatial error with motor judgments was significantly larger than with perceptual judgments. Both induced motion and real motion produced sensorimotor extrapolation. With real motion, the net extrapolation is the difference between perceptual and motor judgments. With induced motion, the difference between perceptual and motor judgment reflects both sensorimotor extrapolation and an illusory shift of the target position. Results were not affected by whether the delay between target offset and response completion/probe onset were matched (A) or not matched (B).

motor extrapolation or an illusory position shift. Previous reports indicated that reaching movements to targets undergoing induced motion are not, or are only slightly, affected by the illusory position shift [1, 11]. Therefore, one possibility is to attribute the complete spatial error to sensorimotor extrapolation. A more conservative approach would assume that sensorimotor extrapolation was about as strong with real as with induced motion, because the two conditions were perceptually indistinguishable. To estimate the size of the illusory position shift, we therefore subtracted the net sensorimotor extrapolation in the real-motion condition from the difference between perceptual and motor conditions in the induced-motion condition. The illusory position shift was 0.82 ± 0.1 deg and significantly different from zero ($p < 0.0005$), but only 20%–27% of the average illusory motion path of 3 deg. Thus, motor judgments were clearly affected by induced motion, but in agreement with previous studies, they were not completely misled. In contrast, retinotopic position judgments were not affected at all by induced motion. Again, this shows that the sensorimotor system is not always immune to illusions compared to cognitive/perceptual judgments. Quite the opposite was true: reaching endpoints showed larger deviations from the true target position. With induced motion, the error may be the combined product of induced position shifts in egocentric space and sensorimotor extrapolation of target position.

In contrast to experiment 1, perceptual judgments were displaced in the direction of motion with real motion. The reason for this error was that the eye followed the target with a gain of 0.78 ± 0.02 deg and continued to move after target offset (overshoot). In the perceptual condition, the oculomotor overshoot was 0.37 ± 0.04 deg when the probe stimulus appeared. In the motor condition, it was 0.47 ± 0.04 deg when the finger made contact with the screen. The localization error after oculomotor overshoot in the direction of motion has long been known and may be attributed to visible persistence [15] or a failure to match retinal and extraretinal signals [16].

Conclusions

In sum, we show that the sensorimotor system extrapolates the position of moving objects into the future, whereas the perceptual/cognitive system represents the target position accurately. Sensorimotor extrapolation may compensate for neuronal delays and assures that goal-directed movements are accurate. This proposal differs significantly from previous accounts in that we do not believe that early visual processes solve the problem of neuronal delays. Even though visual extrapolation of target motion offers a plausible solution, it is disproved by correct endpoint localization with perceptual judgments. Other proposals, such as shortened latencies for moving objects [6, 17], only alleviate the problem but do not solve it. Further, we show that sensorimotor extrapolation occurs at late stages in motion processing because it was also observed with induced motion that arises from the combination of target and context elements in the absence of retinal motion. We suggest that the problem of neuronal delays is solved when retinotopic information is transformed into an egocentric representation of space. This transformation may be learned. Sensorimotor transformations have been shown to be highly adaptive [18, 19] such that the sensorimotor system may have learned to extrapolate positions in order to be accurate, even if this was accompanied by a loss in precision. The present results, of course, do not rule out that there are instances where motor judgments are more accurate than perceptual judgments. For instance, perisaccadic errors in object localization occur with perceptual judgments, but not with reaching movements [20]. Rather, the present results support the notion that the outcome of early visual processes may be differently used in visuo-motor transformations and visual cognition [8].

Experimental Procedures

The stimuli were presented on a 21 in CRT display (ELO Touchsystems, Fremont, California, USA) with a refresh rate of 100 Hz and a resolution of 1280 (H) $\times$ 1024 (V) pixels. The ELO Entuitive monitor recorded the touched screen position at the display resolution. The monitor had a very low background luminance (less than 0.001 cd/m^2, S370 Optometer, UDT Instruments, Baltimore, Maryland) such that the edges of the display became faintly visible only after about 20 min in the dark. To prevent complete dark adaptation, the experiment was run in short blocks of 10–15 min. All stimuli were dark gray (0.18 cd/m^2). Observers' head position was stabilized with a chin rest at 47 cm from the screen. Eye movements were recorded with a head-mounted, video-based eye tracker (EyeLink II, SR-Research, Osgoode, Ontario, Canada).

Observers triggered stimulus and motion onset by pressing a key about 20 cm from the touch screen. In the motor condition, participants were instructed to keep the home key depressed until target offset. Then, they pointed toward the final target position as rapidly and accurately as possible. If the time interval between target offset and contact with the screen, referred to as movement time, was larger than 1.3 s, an error message appeared. In the perceptual condition, a probe stimulus appeared 0.5 or 1 s after target offset and remained visible until a response was emitted. The probe positions jittered around the true final position. Participants indicated by mouse click whether the probe appeared in the same position as the target or not.

In experiment 1, fixation on the central fixation mark was monitored during stimulus presentation, and fixation errors were reported to the participant. After target offset, observers were free to move their eyes. There was no consistent eye movement pattern across or within participants: sometimes observers maintained fixation, and sometimes they made a saccade to the target position. The target was a 0.6 deg disk that appeared 15 deg to the left or right and 8 deg below the fixation point. It moved horizontally at 11.3, 18.8, or 26.3 deg/s toward the opposite side and vanished randomly within 8.5 deg to the left or right of central fixation. Probes were offset by $\pm$1.6, $\pm$0.5, and 0 deg from the true final position. Negative numbers indicate probe deviations opposite to the direction of target motion. In one version of the experiment, the fixation mark was turned off with the target ($n = 7$), whereas it remained visible until a response was given in the other ($n = 8$).

Each participant in experiment 1 worked through 198 trials in the motor and 315 trials in the perceptual condition. The order of conditions was approximately balanced across observers. Students at the Justus-Liebig-University of Giessen were paid for their participation, reported normal or corrected-to-normal vision, and were naive as to the purpose of the experiment.

In experiment 2, smooth pursuit eye movements and eye fixation were recorded. The target was surrounded by a large 18 $\times$ 6 deg unfilled rectangle (referred to as frame). Either the target (real motion) or the frame (induced motion) followed a sinusoidal trajectory of 4.5 deg amplitude and 0.05 Hz temporal frequency. The maximal velocity was 1.4 deg/s. The target's initial position was 3 deg from the frame's center. The target always moved or appeared to move toward the frame's center and vanished within 1.5 deg of the center. Target and frame disappeared simultaneously. The center of the stationary object (target or frame) was randomly placed within 5 deg left or right and 10 deg below the screen center. Participants were instructed to fixate the target.

Experiment 2 was run with two different temporal parameters. In one version, there were no temporal constraints on motor judgments and the probe for perceptual judgments appeared 0.5 s after target offset ($n = 8$). In the second version, motor judgments had to be completed within 1.3 s, and the probe for perceptual judgments appeared 1 s after target offset ($n = 7$). The deviation of the motor response or the probe positions ($\pm$1, $\pm$0.5, and $\pm$0 deg) from the true final position are expressed with respect to the perceived (real or induced) direction of motion. Participants were instructed to fixate the target and worked through 120 trials in the perceptual task and 132 trials in the motor task. Because two students participated in both versions of the experiment, the data could not be collapsed as in experiment 1.

Because of faulty eye movement recording, eye blinks, saccades, and early or late responses, 6%–9% of the data were discarded in experiment 1 and between 1%–3% (perceptual condition) or around 6% (motor condition) in experiment 2. In the motor condition, the deviation of the judged from the true position was calculated as an index of the judged final target position. Reaching responses were well correlated with the true final target position. Because there was no visual feedback, some observers showed a shift of the subjective straight ahead direction in their reaching movements. Maximum mean deviations exhibited by single participants were 3.3 deg to the right and 2.2 deg to the left. However, the mean straight-ahead shift across participants was 0.2 $\pm$ 0.4 deg (n.s.) to the right. Because leftward and rightward target motion was equally likely, effects of straight-ahead shifts on the spatial error would cancel out. For instance, a subject pointing too far to the left by 2 deg with sensorimotor extrapolation of 1 deg would have a spatial error of +3 deg in the direction of motion with a target traveling to the left (errors add up) and a spatial error of −1 deg opposite to target motion with a target traveling to the right (errors cancel). The average, however, of +3 deg and −1 deg would be +1 deg, which accurately reflects the sensorimotor extrapolation. In the perceptual condition, a cumulative normal distribution was fit to the proportion of same judgments. The expectancy value of the distribution, μ, estimated the point of subjective equality between final target and probe position.

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References

1. Smeets, J.-B.J., and Brenner, E. (1995). Perception and action are based on the same visual information: distinction between position and velocity. J. Exp. Psychol. Hum. Percept. Perform. *21*, 19–31.
2. Nijhawan, R. (1994). Motion extrapolation in catching. Nature *370*, 256–257.
3. Krekelberg, B., and Lappe, M. (2001). Neuronal latencies and the position of moving objects. Trends Neurosci. *24*, 335–339.
4. Nijhawan, R. (2002). Neural delays, visual motion and the flash-lag effect. Trends Cogn. Sci. *6*, 387.
5. Whitney, D., Murakami, I., and Cavanagh, P. (2000). Illusory spatial offset of a flash relative to a moving stimulus is caused by differential latencies for moving and flashed stimuli. Vision Res. *40*, 137–149.
6. Whitney, D., and Murakami, I. (1998). Latency difference, not spatial extrapolation. Nat. Neurosci. *1*, 656–657.
7. Eagleman, D.M., and Sejnowski, T.J. (2000). Motion integration and postdiction in visual awareness. Science *287*, 2036–2038.
8. Goodale, M.A., and Milner, A.D. (1992). Separate visual pathways for perception and action. Trends Neurosci. *15*, 20–25.
9. Bridgeman, B., Peery, S., and Anand, S. (1997). Interaction of cognitive and sensorimotor maps of visual space. Percept. Psychophys. *59*, 456–469.
10. Glover, D. (2003). Separate visual representations in the planning and control of action. Behav. Brain Sci., in press.
11. Bridgeman, B., Kirch, M., and Sperling, A. (1981). Segregation of cognitive and motor aspects of visual function using induced motion. Percept. Psychophys. *29*, 336–342.
12. Milner, D., and Dyde, R. (2003). Why do some perceptual illusions affect visually guided action, when others don't? Trends Cogn. Sci. *7*, 10–11.
13. Franz, V.H. (2001). Action does not resist visual illusions. Trends Cogn. Sci. *5*, 457–459.
14. Mack, A., Heuer, F., Fendrich, R., Vilardi, K., and Chambers, D. (1985). Induced motion and oculomotor capture. J. Exp. Psychol. Hum. Percept. Perform. *11*, 329–345.
15. Kerzel, D. (2000). Eye movements and visible persistence explain the mislocalization of the final position of a moving target. Vision Res. *40*, 3703–3715.
16. Brenner, E., Smeets, J.B., and van den Berg, A.V. (2001). Smooth eye movements and spatial localisation. Vision Res. *41*, 2253–2259.
17. Purushothaman, G., Patel, S.S., Bedell, H.E., and Ogmen, H. (1998). Moving ahead through differential visual latency. Nature *396*, 424.
18. Stratton, G.M. (1897). Vision without inversion of the retinal image. Psychol. Rev. *4*, 463–481.
19. Bedford, F.L. (1999). Keeping perception accurate. Trends Cogn. Sci. *3*, 4–11.
20. Burr, D.C., Morrone, M.C., and Ross, J. (2001). Separate visual representations for perception and action revealed by saccadic eye movements. Curr. Biol. *11*, 798–802.